

## Positive Allometry for Caste Size Dimorphism in *Pheidole* Ants: A New Form of Interspecific Allometry

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**Abstract.**—Alternative phenotypes that differ in body size, shape or other attributes coexist in many animal species, with male-female differences being the most familiar form of alternative phenotypes. Ants are an unappreciated ideal model system to explore allometric interrelationships among alternative phenotypes. Seven different forms of size dimorphism occur within ants, including dimorphisms within and between males and females. In this study I show that a pattern of body size dimorphism parallel to Rensch's rule is found in at least one form of *intra*-sexual dimorphism, that of the sterile worker castes of ants in the genus *Pheidole*. I compared the head and pronotum size of major and minor workers of 105 species of New World *Pheidole* that span the entire range of body size in this genus. Head size of major and minor workers was highly correlated across species ( $r = 0.84$ ,  $P < 0.001$ ), as was pronotum size of the two castes ( $r = 0.82$ ;  $P < 0.0001$ ). Standardized major axis regression of log(head width of major worker) against log(head width of minor worker) showed extreme positive allometry with a slope ( $\beta$ ) of 1.53 (95% CI = 1.37–1.71), whereas the analogous regression for pronotal width showed significantly less positive allometry with a slope ( $\beta$ ) of 1.22 (95% CI = 1.10–1.37). When adjusted for phylogenetic autocorrelation using phylogenetically independent contrasts, head width allometry was still strongly positive ( $\beta = 1.36$ , 95% CI = 1.21–1.54), whereas pronotal width allometry was isometric  $\beta = 1.09$ , 95% CI = 0.94–1.26). I propose several hypotheses to account for positive caste size allometry in ants and suggest that testing them may help point the way to a general class of explanations that encompass both inter- and intrasexual forms of size dimorphism.

**Key words.**—ants, allometry, caste dimorphism, comparative analysis, phylogenetic analysis, *Pheidole*

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Discrete phenotypic classes that differ in adult size, shape or other morphological attributes often coexist within species. These different phenotypic classes may arise from allelic differences among individuals (genetic polymorphisms) or from developmentally induced differences in gene expression in response to different environments experienced by individuals (polyphenisms) (Stern and Emlen 1999; Emlen 2000; Emlen and Nijhout 2000; Evans and Wheeler 2001). Familiar examples of such discrete phenotypic classes include male-female differences in nearly every animal group, alary dimorphism in both male and female insects (Harrison 1980; Roff 1986), size and armament di-

morphism in males (Thornhill and Alcock 1983; Fairbairn 1997 and references therein; Emlen and Nijhout 2000), and the sterile and reproductive castes of social insects (Wilson 1971). While these forms of phenotypic dimorphism may have different underlying genetic or developmental origins, all of them presumably evolved, differentiated and persist in species due to the action of natural selection alone or in combination with other evolutionary forces. A major challenge of evolutionary ecology is to identify the evolutionary, developmental and ecological contexts in which these phenotypic classes arise (Emlen and Nijhout 2000; Evans and Wheeler 2001).

The extent of differences among phenotypic classes can vary widely within an evolutionary lineage. For example, quantitative studies of male-female differences in body size, or sexual size dimorphism (SSD), within related groups of organisms often reveal allometric trends in SSD. Abouheif and Fairbairn (1997) have shown that many independent lineages follow a pattern known as “Rensch’s rule” (Rensch 1950, 1959): in clades in which females tend to be the larger sex, SSD diminishes in larger species (but see Webb and Freckleton 2007), whereas in clades in which males are the larger sex, SSD increases in larger species. Both these patterns are the result of greater size variation in males relative to females among species in an evolutionary lineage. The underlying causes of these patterns of interspecific allometry are still actively debated (e.g. Blanckenhorn et al. 2007; Webb and Freckleton 2007), but the emerging consensus is that Rensch’s rule is the product of differences in selective pressures faced by the two sexes and the underlying genetical or selectional correlations between them (Fairbairn 1997).

Alternative phenotypes also occur *within* one sex in many species. In contrast to SSD, however, patterns of interspecific allometry of intrasexual forms of dimorphism have received little quantitative analysis. These forms of dimorphism, however, offer unexploited opportunities for allometric studies and raise a variety of interesting questions about the evolutionary relationships among alternative phenotypes. Do these intrasexual forms of dimorphism exhibit allometric patterns similar to those described by Rensch’s rule? How are allometric patterns of size dimorphism correlated in species with multiple forms of size dimorphism? That is, do the different forms of size dimorphism share the same allometric patterns? How different are the patterns in different evolutionary lineages? What are the underlying microevolutionary processes that give rise

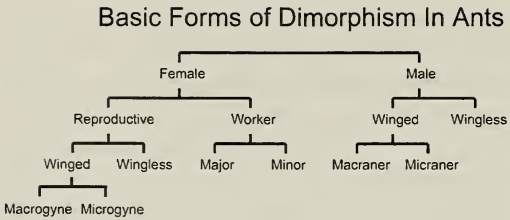


Fig. 1. Basic types of dimorphism in ants. Body size of male and female reproductives is highly variable across species. While females are always larger than males, the difference in size between the sexes is immense in some species and nearly nonexistent in other species. Size differences between female reproductives and female sterile workers are also highly variable among species. In species with dimorphic sterile castes body size of major workers is always larger than body size of minor workers, but species differ in the extent of this size dimorphism. Dimorphism in males is less common in ants than other forms of dimorphism.

to these different macroevolutionary patterns?

Ants are an ideal model system in which to examine interspecific allometric patterns of body size dimorphism and inter-relationships among them. All ants are eusocial with distinct reproductive (male and female) and non-reproductive (sterile female worker) castes (Hölldobler and Wilson 1990). Seven different forms of body size dimorphism exist within ants (Fig. 1). Some of these forms are universal or nearly so, such as the dimorphism between male and female reproductive castes and the dimorphism between reproductive and sterile castes in females (Hölldobler and Wilson 1990; Stubblefield and Seger 1994). Other forms are less ubiquitous, but are nonetheless common enough for comparative analysis. Approximately 15% of all ant genera (45/297) show some degree of size variation or polymorphism in the sterile worker caste (Oster and Wilson 1978). Complete worker dimorphism has evolved independently in at least eight lineages, wherein the two distinct worker subcastes are referred to as major and minor workers. In most species, majors are distinguished from minors by their larger bodies, disproportionately larger heads, and



behavioral specialization (Hölldobler and Wilson 1990). In addition to the plethora of dimorphic forms available in ants, another advantage ants offer allometric studies of body size dimorphism is the great degree of variability in size dimorphism across species. For example, SSD can vary over several orders of magnitude, while mass differences in body size between major and minor workers can vary by up to a factor of 500 (Stubblefield and Seger 1994).

In this paper, I show for the first time that positive interspecific allometry for size dimorphism exists between the sterile worker subcastes of the ant genus *Pheidole*. That is, caste dimorphism is greater in larger species than it is in smaller species. Such an evolutionary pattern of size dimorphism may have a profound effect on how colony labor is divided between worker subcastes in this genus. *Pheidole* (Subfamily Myrmicinae), with over 900 described species, is by far the largest genus with dimorphic worker castes (Bolton 1995; Wilson 2003). In colonies with a normal complement of queens and brood, minor workers perform 30–40 distinct tasks, including those associated with brood and queen care, nest maintenance, foraging and defense (Wilson 1984; Hölldobler and Wilson 1990). Major workers, in contrast, normally perform only 20–70% the number of tasks of minor workers, and appear to be particularly poor at rearing brood (Wilson 1984; Hölldobler and Wilson 1990; Sempo and Detrain 2004). In this genus major workers are apparently specialized for three primary, often mutually exclusive, functions: seed processing, nest site and resource defense, or food storage (Creighton 1966; Wilson 1984; Feener 1987; Hölldobler and Wilson 1990). Behavioral specialization is carried to even greater extremes in some species. For example, major workers of *Pheidole dentata* defend the colony against ants in the genus *Solenopsis*, but they normally do not defend the colony against other ants species (Wilson 1976a, b; Feener 1981) unless they

are repeatedly exposed to them (Carlin and Johnston 1984). In the discussion I propose several possible hypotheses that could account for these allometric patterns and suggest further studies of the various forms of body size dimorphism in ants may point the way toward a general class of explanations that encompass all forms of size dimorphism.

In addition to documenting the existence of positive interspecific allometry for caste size dimorphism in the ant genus *Pheidole*, I also evaluate the utility of randomly constructed phylogenies in testing comparative hypotheses (Martins 1996). This technique has been criticized on several grounds (Donoghue and Ackery 1996; Martins 1996; Abouheif 1998), but may nonetheless be useful in the absence of phylogenetic relationships of focal taxa. Here I show that the use of random phylogenies in the analysis of caste size dimorphism in *Pheidole* compares favorably to the analysis based on the known phylogeny. I conclude that random phylogenies can indeed be useful in comparative studies, despite their limitations.

## MATERIALS AND METHODS

I examined interspecific allometry for caste dimorphism in 105 species of *Pheidole* from North and South America (Appendix 1) (Wilson 2003). These species were selected because they were included in the recent phylogenetic analysis of *Pheidole* by Moreau (2008) so that their evolutionary relationships are known. Conveniently, these species also span the entire range of body size found in the genus. For each of these species I took the measurements of head width (HW) and pronotal width (PW) for major and minor workers from the descriptions in Wilson (2003). Measurements of each caste are from one individual, often the holotype, paratype or lectotype. Intraspecific variation was ignored in this study. Four of the species included in this study (*obtusospinosa*, *polymorpha*, *rhea*

and *tepicana*) possess a supermajor subcaste in addition to major and minor workers (Wilson 2003). This subcaste was not included in analyses.

I estimated interspecific allometry for caste size dimorphism by regressing the  $\log(\text{major worker size})$  against  $\log(\text{minor worker size})$  for both head width and pronotal width. I used standardized major axis (SMA) regression to estimate the allometric coefficient ( $\beta$ ), or the slope of the regression, and its confidence limits (Model II in Sokal and Rohlf 1995). SMA regression is more appropriate than ordinary least squares regression for data in which both X and Y variables are subject to random error as is the case in most allometric studies (McArdle 1988; LaBarbera 1989; Sokal and Rohlf 1995). SMA regression is also preferable to major axis regression because it is generally more efficient and less biased under a wide range of error variances (McArdle 1988). Calculation of SMA intercept, slope, their confidence intervals (CI) and significance testing followed the recommendations of Warton et al. (2006), using the *R* statistics package *smatr* (Warton et al. 2006).

Regression statistics were calculated for raw, phylogenetically uncorrected data and for phylogenetically independent contrasts (Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991; Martins and Garland 1991; Grafen 1992; Pagel 1992; Purvis et al. 1994) as calculated from the phylogenetic relationships of the 105 species included in the study. I used the "pic" command in the *R* statistics *ape* package to calculate 104 phylogenetically independent contrasts (Paradis 2006). Regressions for the phylogenetically independent contrasts were forced through the origin as recommended by Garland et al. (1992). There was no evidence of non-linearities in these relationships which would invalidate this procedure (Quader et al. 2004).

To further analyze how caste dimorphism changes with body size, I calculated

a caste dimorphism index (CDI) that is analogous to the sexual dimorphism index (SDI) of Lovich and Gibbons (1992). I defined  $CDI = \log(\text{major worker size}) - \log(\text{minor worker size})$ .

In the absence of a known phylogeny, Martins (1996) recommended using "random" phylogenies to account for phylogenetic autocorrelation. Despite its limitations (Donoghue and Ackerly 1996; Martins 1996; Abouheif 1998), this procedure is potentially very useful in testing comparative hypotheses in lineages for which phylogenetic relationships are not yet known. To see how useful Martins's procedure would be in the present study, I compared the results of randomly generated phylogenies against the results of the known phylogeny by generating two random sets of 1000 phylogenetic trees, one assuming a "standard" time only model of speciation and the other assuming a "coalescent" model of speciation (see Martins 1996 for differences between these models). For each random tree I then generated 104 independent contrasts in head width and pronotal width for major and minor workers. I then performed SMA regression analyses on these independent contrasts to estimate the allometric coefficient ( $\beta$ ) and its confidence limits (CIs). These regressions were forced through the origin as they were for the known phylogeny (Garland et al. 1992). Confidence intervals (CI) of the mean  $\beta$  for 1000 trees were estimated by ordering the slope values and taking the lowest 2.5% value as the low confidence limit and taking the highest 2.5% value as the high confidence limit. Randomized trees were generated using the "rtree" and "rcoal" commands in the *R* statistics *ape* package, for standard and coalescent models of speciation, respectively (Paradis 2006). Phylogenetically independent contrasts and regression analysis were calculated as above for the known phylogeny.



## RESULTS

### Analysis of Phylogenetically Uncorrected Data

Head width of major workers was 5.4 times more variable than head width of minor workers across the 105 species included in this study (coefficients of variation for log-transformed data were 1.79 for major workers vs. 0.33 for minor workers). Despite the difference in size variation, head width of major workers was nevertheless strongly correlated with head width of minor workers ( $r = 0.84$ ,  $P < 0.001$ ; Fig. 2A). Phylogenetically uncorrected interspecific allometry for caste size dimorphism in head width showed strong positive allometry (Table 1; Fig. 2A). The allometric slope of the SMA regression ( $\beta = 1.53$ , 95% CI = 1.37–1.71) was significantly greater than 1.00 ( $P < 0.001$ ). Such positive allometry means that larger species are more caste dimorphic than smaller species, as indicated by the significant positive correlation ( $r = 0.26$ ,  $P = 0.007$ ) between the caste dimorphism index (CDI) and log(head width of minor workers) (Fig. 2B).

Pronotal width of major workers was only 2.4 times more variable than pronotal width in minor workers (coefficients of variation for log-transformed data were 0.53 for major workers vs. 0.22 for minor workers). The correlation among subcastes for pronotal width was similar to that found for head width ( $r = 0.82$ ,  $P < 0.0001$ ; Fig. 2C). As with head width, phylogenetically uncorrected interspecific allometry for caste size dimorphism in pronotal width was strongly positive (Table 1; Fig. 2C). The allometric slope of the SMA regression ( $\beta = 1.22$ ; 95% CI = 1.10–1.37) was significantly greater than 1.00 ( $P < 0.0007$ ), but the CDI showed no significant correlation with log(pronotal width of minor workers) ( $r = 0.03$ ,  $P = 0.7$ ; Fig. 2D). Although the slopes for both head width and pronotal width allometry were signif-

icantly greater than 1.00, the slope for pronotal width was significantly less than that for head width ( $P = 0.0002$ ). This means that across species, head width dimorphism increases more steeply with size than pronotal width.

### Analysis of Phylogenetically Independent Contrasts

Results of regression analyses of the independent contrasts derived from Moreau's phylogenetic tree qualitatively supported the results derived from the non-phylogenetic analyses (Table 1 and Fig. 3). Independent contrasts of head width of major and minor workers were strongly correlated with one another ( $r = 0.78$ ,  $P < 0.001$ ; Fig. 3A) and showed strong positive allometry (Table 1; Fig. 3A). The allometric slope of the SMA regression ( $\beta = 1.36$ , 95% CI = 1.21–1.54) was less than that for the phylogenetically uncorrected data, but it was still significantly greater than 1.00 ( $P < 0.001$ ). Independent contrasts of pronotal width of major and minor workers were also strongly correlated with one another ( $r = 0.66$ ,  $P < 0.001$ ; Fig. 3B), but their relationship was now isometric rather than positively allometric as it was for the phylogenetically uncorrected data (Table 1; Fig. 3B). The allometric slope of the SMA regression ( $\beta = 1.09$ , 95% CI = 0.94–1.26), did not differ significantly from 1.00. Just as seen in the phylogenetically uncorrected data, the slope for pronotal width was significantly less than that for head width ( $P = 0.003$ ), reinforcing the conclusion that across species, head width dimorphism increases more steeply with size than pronotal width dimorphism.

Analysis within castes of the interspecific allometry for head width versus pronotal width revealed two underlying patterns that contributed to the positive allometry for caste dimorphism described above (Fig. 4). First, allometry for log(head width) on log(pronotal width) in major workers was weakly positive or isometric ( $\beta = 1.11$ , 95% CI = 1.04–1.19 for raw data;

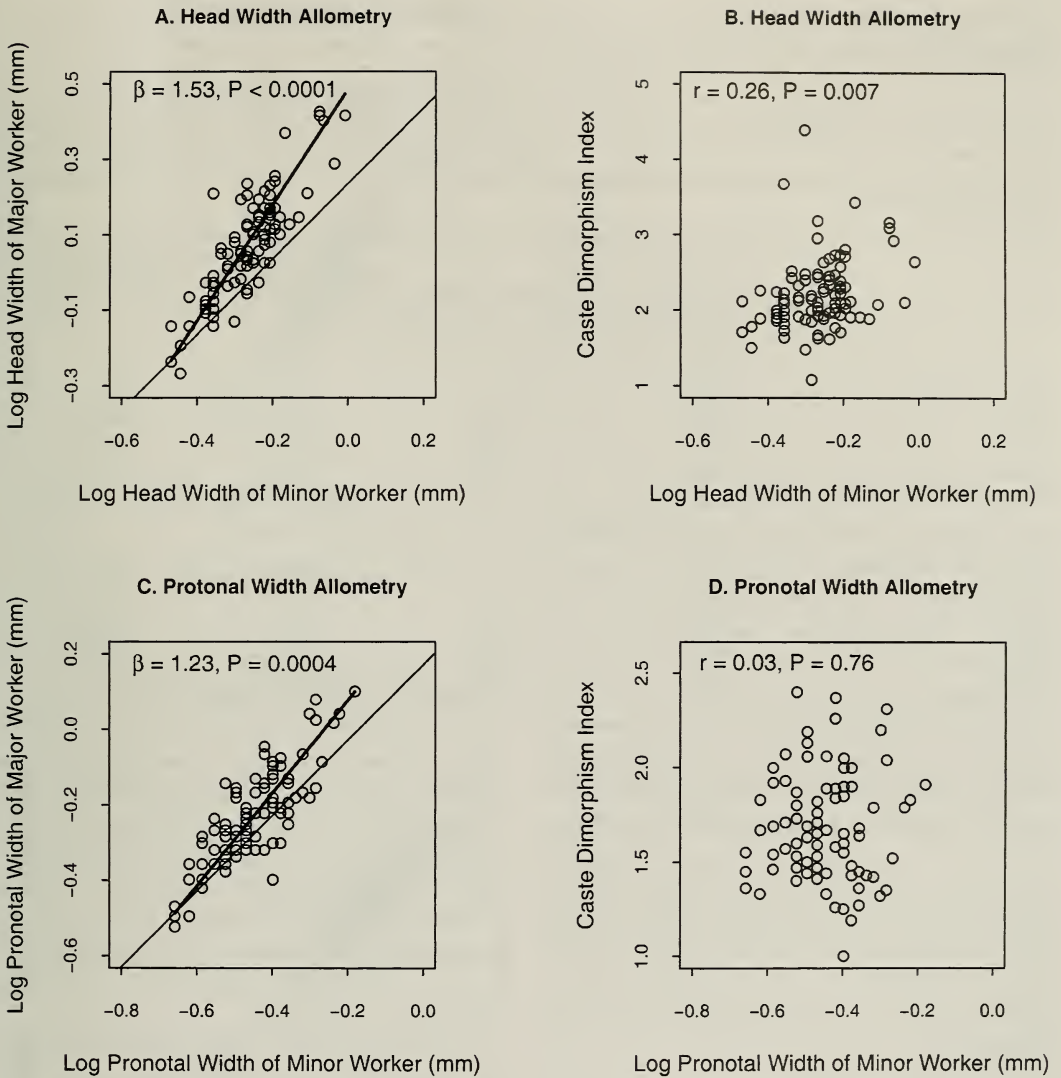


Fig. 2. Phylogenetically uncorrected allometric relationships between major and minor worker castes in New World members of the ant genus *Pheidole* ( $n = 105$  species). Heavy solid line is SMA regression line, light solid line is isometry reference line of  $\beta = 1$ . A. Interspecific allometry for caste size dimorphism using head width as a measure of body size. Equation for the SMA regression is:  $\log(\text{head width of major worker}) = -0.58 + 1.53[\log(\text{head width of minor worker})]$ ,  $r = 0.84$ . Slope of the line is significantly greater than 1.00 ( $P < 0.0001$ ). B. Correlation between the index of caste dimorphism and  $\log(\text{head width of minor workers})$ ,  $r = 0.26, P < 0.007$ . C. Interspecific allometry for caste size dimorphism using pronotal width as a measure of body size. Equation for the SMA regression is  $\log(\text{pronotal width of major worker}) = -0.34 + 1.23[\log(\text{pronotal width of minor worker})]$ ,  $r = 0.82$ . Slope of the line is significantly greater than 1.00 ( $P = 0.0004$ ). D. Correlation between the caste dimorphism index and  $\log(\text{pronotal width of minor workers})$ ,  $r = 0.03, P = 0.76$ .

$\beta = 1.09$ , 95% CI = 0.99–1.21 for phylogenetically independent contrasts), which means that relative to pronotal width major workers have slightly disproportionately or proportionately *larger* heads in

larger species. Second, this same allometry in minor workers was strongly negative ( $\beta = 0.89$ , 95% CI = 0.83–0.95 for raw data;  $\beta = 0.87$ , 95% CI = 0.79–0.97 for phylogenetically independent contrasts), which



Table 1. Summary statistics for the slope of SMA regressions of A. log(head width of major worker) on log(head width of minor worker) and B. log(pronotal width of major worker) on log(pronotal width of minor worker). Uncorrected data were not adjusted for phylogenetic “non-independence.” Independent contrasts were adjusted for phylogenetic “non-independent”. Random independent contrasts were based on 1000 randomly generated phylogenies that assumed either a standard speciation model or a coalescent speciation model (see Martins 1996, 1999 and Paradis 2006 for details).  $Var_P$  is the variance resulting from uncertainty in the phylogeny and  $Var_S$  is the variance resulting from deviations of the species data points from the predicted model (Martins 1996).

Statistic	Uncorrected data	Independent contrasts	Random independent contrasts	
			Standard model	Coalescent model
A. Regression for head width of major workers on head width of minor workers				
Correlation coefficient	0.84	0.78	0.83	0.81
Slope estimate	1.53	1.36	1.50	1.55
Var <sub>P</sub>	0.0000	0.0000	0.0098	0.7593
Var <sub>S</sub>	0.0069	0.0068	0.0069	0.0144
Total se	0.0830	0.0826	0.1295	0.8796
95% confidence interval	1.37 < β < 1.71	1.21 < β < 1.54	1.32 < β < 1.69	0.94 < β < 2.32
B. Regression for pronotal width of major workers on pronotal width of minor workers				
Correlation coefficient	0.82	0.66	0.84	0.84
Slope estimate	1.23	1.09	1.27	1.31
Var <sub>P</sub>	0.0000	0.0000	0.0067	0.1476
Var <sub>S</sub>	0.0048	0.0066	0.0046	0.0057
Total se	0.0690	0.0810	0.1062	0.3915
95% confidence interval	1.10 < β < 1.37	0.94 < β < 1.26	1.13 < β < 1.43	0.81 < β < 2.07

means that relative to pronotal width minor workers have disproportionately *smaller* heads in larger species. Any hypothesis advanced to explain positive allometry for caste dimorphism should account for both the slight positive allometry or isometry in relative head size of major workers, and the strong negative allometry in relative head size in minor workers.

Random Phylogenies

Correlation coefficients and slope estimates from the randomly generated phylogenies were nearly identical to the phylogenetically uncorrected values (Table 1). The underlying speciation model used to construct the phylogenetic trees had little effect on mean slope estimates or correlation coefficients, but the coalescent model produced substantially wider variance in the distribution of slope values and therefore wider 95% CIs than did the standard model (Table 1 and Fig. 5). The total standard error of the slope estimates for the random phylogenies were substan-

tially larger (1.3–10.6 times) than the estimates for the uncorrected data or the independent contrasts. This increase was due entirely to the added variance associated with phylogenetic uncertainty ( $Var_P$  in Table 1). In fact, variance attributed to deviation of the species data points from the regression model ( $Var_S$ ) was nearly the same for all analyses.

The distributions of slope estimates from the randomly constructed trees were extremely leptokurtic around the mean values of the uncorrected data (Fig. 5). The leptokurtic nature of these distributions kept the empirically derived 95% CIs smaller than they would have been if estimated from normal theory. For head width allometry all the models predicted the same qualitative pattern of significantly positive allometry for head width of major workers plotted against the head width of minor workers. In contrast, the qualitative pattern of pronotal width allometry was isometric in the independent contrasts and the random phylogenies based on the coalescent model, and significantly posi-

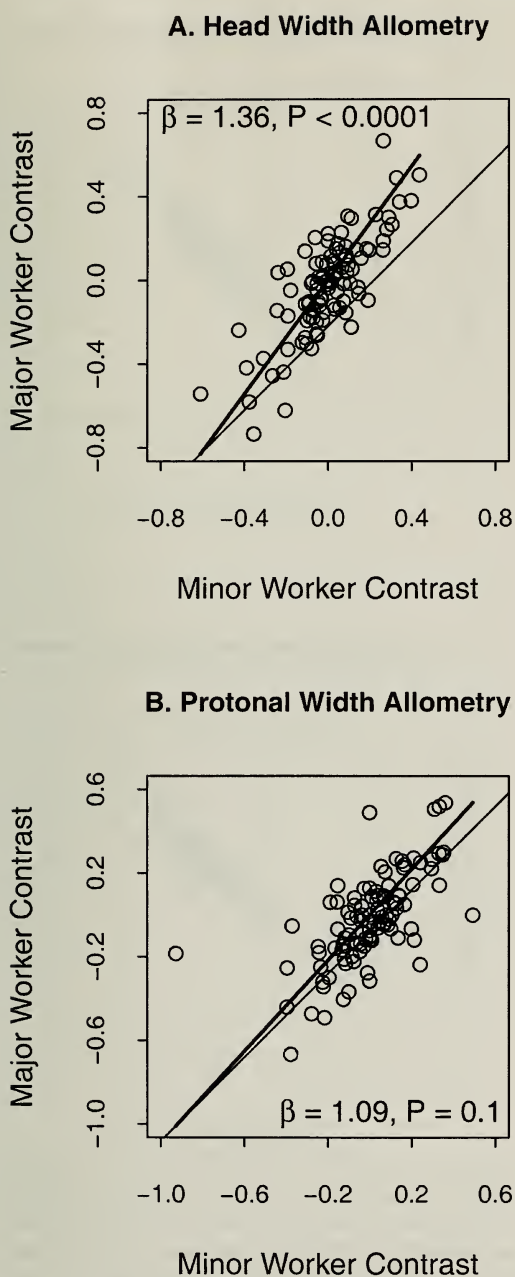


Fig. 3. Allometric relationships of phylogenetically independent contrasts between major and minor worker castes in New World members of the ant genus *Pheidole* ( $n = 104$  contrasts). Heavy solid line is SMA regression line, light solid line is isometry reference line of  $\beta = 1$ . A. Interspecific allometry for caste size dimorphism using head width as a measure of body size. Equation for the SMA regression is: major worker contrast =  $0.00 + 1.36(\text{minor worker contrast})$ ,  $r = 0.79$ . Slope of the line is significantly greater than 1.00 ( $P < 0.0001$ ). B. Interspecific

allometry for caste size dimorphism using pronotal width as a measure of body size. Equation for the SMA regression is: major worker contrast =  $0.00 + 1.08(\text{minor worker contrast})$ ,  $r = 0.66$ . Slope of the line is not significantly different from 1.00 ( $P = 0.1$ ).

## DISCUSSION

Results of this study uncovered three patterns of variation that must be explained in building an understanding of positive allometry for caste size dimorphism in *Pheidole*. First, head size of major workers is more variable among species than head size of minor workers. The greater size variability in major workers yields an allometric coefficient greater than 1.00 when head size of major workers is plotted against head size of minor workers (Fig. 2). Second, despite the greater interspecific variability in head size among major workers, head size of major and minor workers are highly correlated with one another across species (Table 1). Third, allometry for head size against pronotal width in major workers is isometric or weakly positive, whereas allometry for head size against pronotal width in minor workers is strongly negative (Fig. 4).

## Evolutionary Processes Underlying Positive Allometry for Caste Size Dimorphism

An understanding of positive allometry for caste size dimorphism in ants requires that we account for both the greater variance in size of major workers than minor workers and the high correlation in size between castes. Here I argue that diversifying directional selection on colonies has led to the greater size variance in the major worker caste and that the high correlation in size between castes is a product of either a correlated response to selection in the minor worker caste due to

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allometry for caste size dimorphism using pronotal width as a measure of body size. Equation for the SMA regression is: major worker contrast =  $0.00 + 1.08(\text{minor worker contrast})$ ,  $r = 0.66$ . Slope of the line is not significantly different from 1.00 ( $P = 0.1$ ).



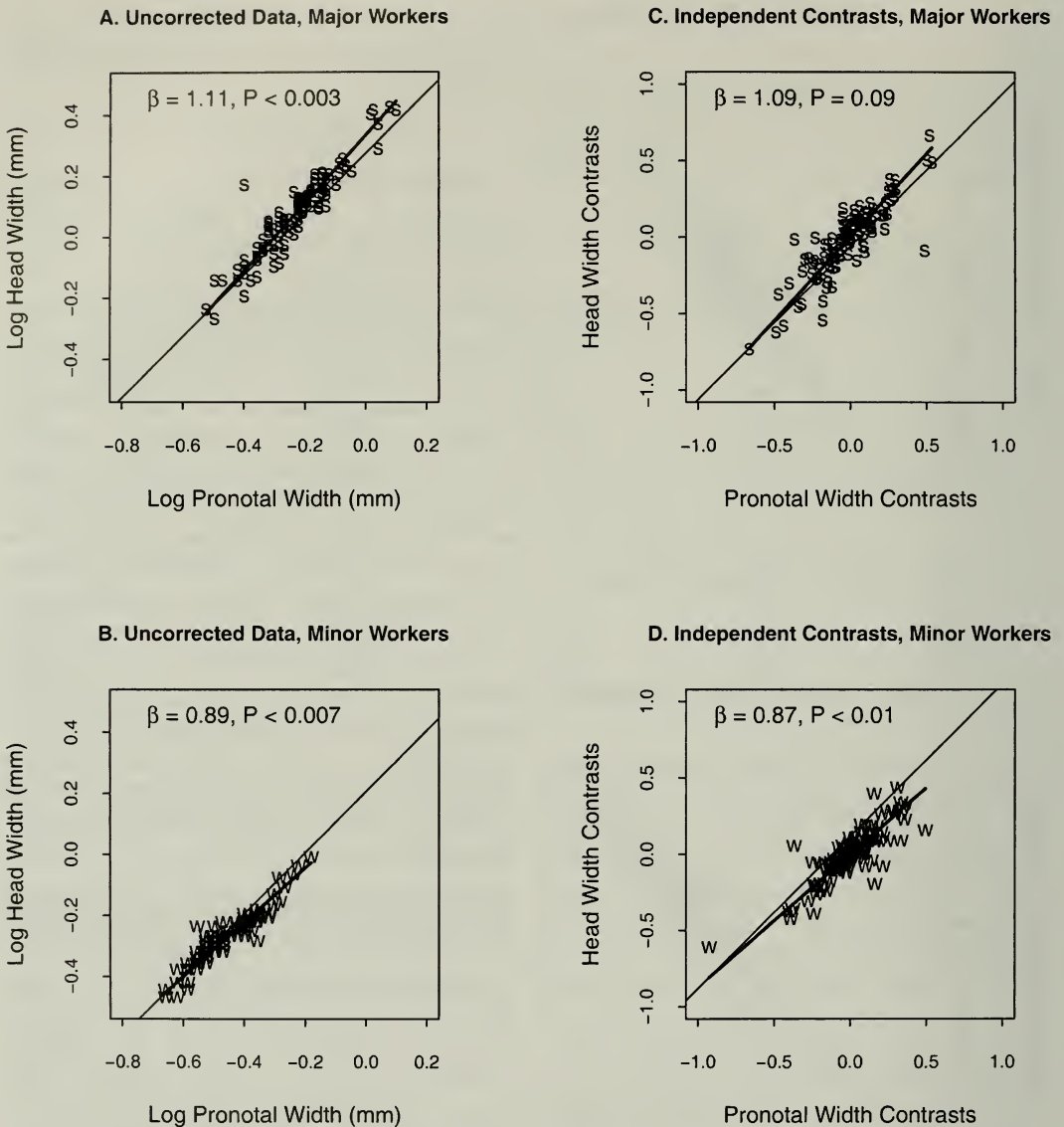


Fig. 4. Allometric relationships of head size versus pronotum size in major and minor workers in New World members of the genus *Pheidole* ( $n = 105$  in A. and B.,  $n = 104$  in C. and D.). Heavy solid line is SMA regression line, light solid line is isometry reference line of  $\beta = 1$ . A. Interspecific allometry of head width versus pronotal width in major workers for raw, uncorrected data. Equation for the SMA regression is:  $\log(\text{head width of major worker}) = 0.33 + 1.11[\log(\text{pronotal width of major worker})]$ ,  $r = 0.93$ . Slope of the line is significantly greater than 1.00 ( $P < 0.003$ ). B. Interspecific allometry of head width versus pronotal width in minor workers for raw, uncorrected data. Equation for the SMA regression is:  $\log(\text{head width of minor worker}) = 0.13 + 0.89[\log(\text{pronotal width of minor worker})]$ ,  $r = 0.94$ . Slope of the line is significantly less than 1.00 ( $P < 0.007$ ). C. Interspecific allometry of head width versus pronotal width in major workers for phylogenetically independent contrasts for major workers. Equation for the SMA regression is:  $\log(\text{head width contrast}) = 0.00 + 1.09[\log(\text{pronotal width contrast})]$ ,  $r = 0.86$ . Slope of the line is significantly greater than 1.00 ( $P < 0.003$ ). D. Interspecific allometry of head width versus pronotal width in major workers for phylogenetically independent contrasts for minor workers. Equation for the SMA regression is:  $\log(\text{head width contrast}) = 0.00 + 1.09[\log(\text{pronotal width contrast})]$ ,  $r = 0.84$ . Slope of the line is significantly less than 0.87 ( $P < 0.01$ ).

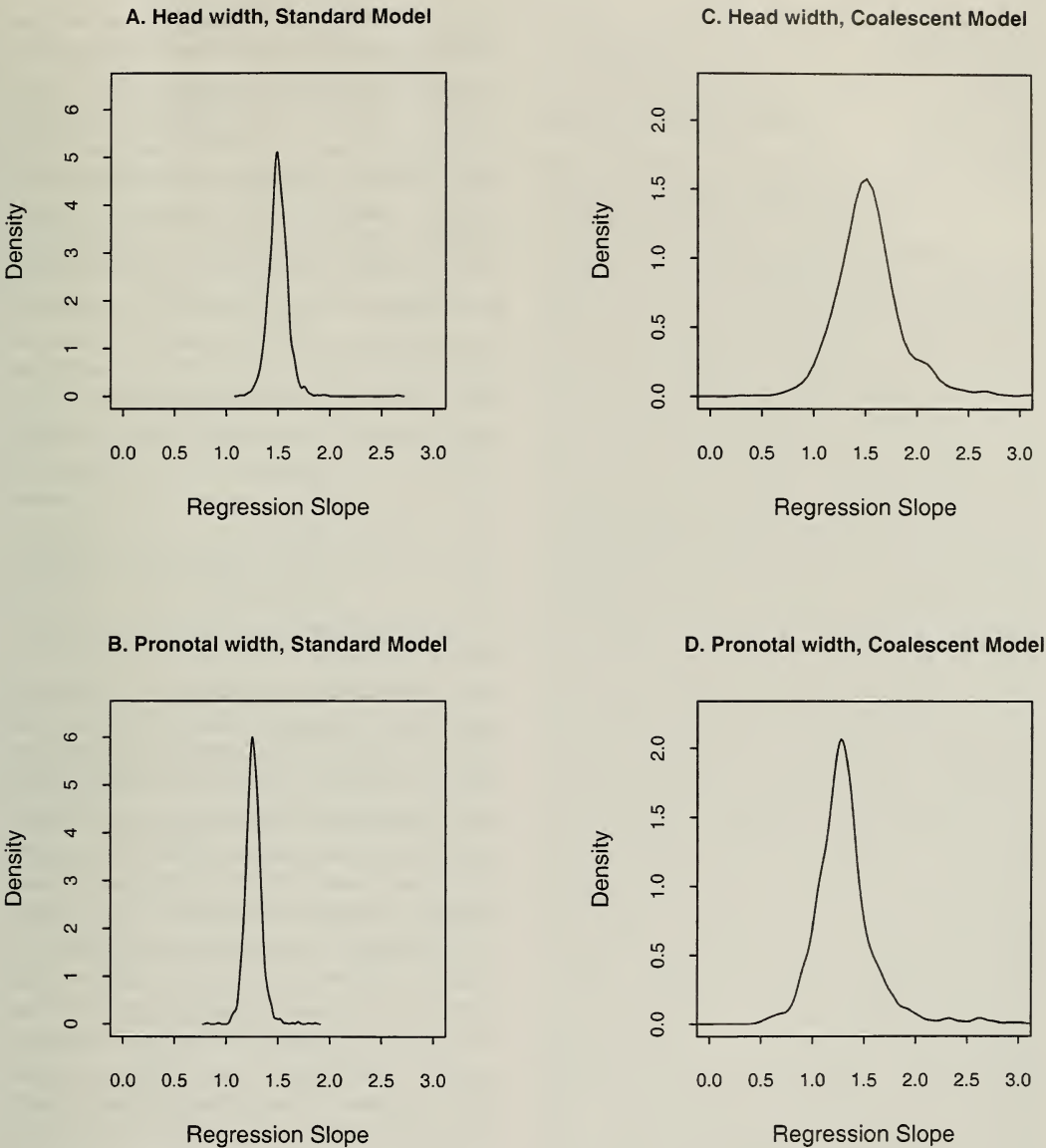


Fig. 5. Distributions of regression slopes derived from 1000 randomly constructed phylogenies. Slope estimate for each phylogeny was based on 104 independent contrasts of 105 species.  $g_2 \pm \text{sek}$  is the kurtosis coefficient and its standard error ( $24/n$ ). A distribution is considered significantly leptokurtic if  $g_2/\text{sek} > 2.00$ . A. Regression slopes for log(head width of major workers) on log(head width of minor workers). Phylogenies assumed standard speciation model.  $g_2 = 22.38 \pm 0.15$ ,  $P < 0.05$ . B. Regression slopes for log(pronotal width of major workers) on log(pronotal width of minor workers). Phylogenies assumed standard speciation model.  $g_2 = 10.29 \pm 0.15$ ,  $P < 0.05$ . C. Regression slopes for log(head width of major workers) on log(head width of minor workers). Phylogenies assumed coalescent speciation model.  $g_2 = 612.88 \pm 0.15$ ,  $P < 0.05$ . D. Regression slopes for log(pronotal width of major workers) on log(pronotal width of minor workers). Phylogenies assumed coalescent speciation model.  $g_2 = 42.65 \pm 0.15$ ,  $P < 0.05$ .



high genetic correlations between castes (Lande 1980) or colony-level correlational selection affecting minor workers as a result division of labor between castes (Zeng 1988).

Major workers in many species of *Pheidole* are specialized to defend their colony's nest site and/or food sources against other colonies of ants (Hölldobler and Wilson 1990). The hypertrophic head of this caste houses large, powerful muscles used to work the mandibles, the most effective weapon major workers have against enemy ants. Within species there may be strong, directional colony-level selection to increase fighting effectiveness of major workers by enlarging the head and thereby enhancing the strength of the mandibles. This hypothesis requires that directional selection intensity on major workers is greater than on minor workers, at least for the behaviors for which majors are specialized. This pattern is likely to be true in general because defense by major workers is often critical to colony survival and reproduction. A similar argument may hold for species in which the major workers are specialized for seed processing. Selection for increased head size and stronger mandibles in major workers of seed harvesting species probably allows access to a greater range of seed size and/or seed coat hardness. In contrast, head size of minor workers may be under strong stabilizing selection as suggested by the strong interspecific negative allometry of head width relative to pronotal width seen in this caste (Fig. 4). A relatively constant head size may be selected as a result of the general nature of the tasks performed by minor workers or their primary role in care of small eggs and larvae (Hölldobler and Wilson 1990). These caste-specific differences in selection pressure may be sufficient to account for the positive allometry in CSD, but they cannot account for the high correlation in size between castes.

As selection acts to increase head size of major workers, head size of minor workers

may also increase through a correlated response to selection due to a high genetic correlation between major and minor workers (Lande 1980, Fairbairn and Preziosi 1994, Fairbairn 1997). Because these castes share a common developmental pathway until late in the last larval instar (Wheeler 1991), genetic correlations between major and minor workers should be as high as or higher than those observed between the sexes (typically  $> 0.80$  for body size, see Lande 1980, Fairbairn 1997). Existence of high genetic correlations between major and minor workers may bias the direction of morphological divergence among species along "genetic lines of least resistance," thus maintaining the phenotypic correlation between castes for long periods of time, even in the face of strong natural selection (Schluter 1996).

An alternative hypothesis for the high correlation between size of major and minor workers is the presence of correlational selection due to the behavioral interactions between worker castes. Proper coordination of division of labor within the colony requires that major and minor workers routinely interact with one another (Hölldobler and Wilson 1990). For example, major and minor workers often exchange food and information with one another through trophallaxis and antennal contact (Hölldobler and Wilson 1990). These necessary interactions make it likely that the efficiency at which each caste performs its duties is not independent of the other caste. Workers that differ too much in size might not be capable of efficient interactions and colony functioning as a whole would therefore suffer. Hence, one might expect that, as head size of major workers increases in response to the defense or seed processing needs of the colony, minor workers would experience correlational selection for increased head size as a result of pressures for efficient interactions among caste members. This hypothesis has the advantage that a high

correlation in size between castes is not only possible at an evolutionary equilibrium, it is expected as an integral part of colony-level efficiency.

Testing the validity of these hypotheses is a major challenge for future work. It will require measurement of genetic correlations between major and minor workers, assessment of caste differences in the intensity of selection under reasonably natural conditions, and a comparison of selection pressures across species that vary in size. A primary goal of this future work should be an explanation of the increasing divergence between castes with an increase in body size.

### Comparative Analysis in the Absence of a Phylogeny

The newly available phylogeny for over 100 species of *Pheidole* (Moreau 2008) provided a unique opportunity to assess the use of randomly constructed phylogenies (Martins 1996) in studies of interspecific allometry. In the present study, analysis of head width allometry using phylogenetically uncorrected data and random phylogenies gave the same qualitative results as an analysis using phylogenetically independent contrasts (Table 1). Similar analyses for pronotal width allometry found that phylogenetically uncorrected data and random phylogenies based on a standard speciation model gave different qualitative results from an analysis using phylogenetically independent contrasts. Results from random phylogenies based on a coalescent model of speciation, however, gave qualitatively similar results to phylogenetically independent contrasts, due to the larger 95% CIs of the coalescent model. While the use of random phylogenies in comparative analysis has several weaknesses (Donoghue and Ackerly 1996; Martins 1996; Abouheif 1998), this study illustrates how cautious application of this approach can be used to test novel comparative hypotheses in lineages lacking phylogenetic information.

### Conclusions

Ants offer unexploited opportunities for comparative studies of body size dimorphism and morphological integration (Pie and Traniello 2006). All free-living species of ants exhibit at least two forms of body size dimorphism: differences between males and reproductive females and differences between reproductive females and sterile worker females. In some species there also may be body size differences in major and minor castes of sterile workers or between winged and wingless males. How these different forms of body size dimorphism are inter-related within and among species has only recently begun (Pie and Traniello 2006). This study demonstrates for the first time that an allometric pattern parallel to Rensch's rule in sexual dimorphic species also holds for the sterile worker castes of ants in the genus *Pheidole*. Results of this study suggest that a size-related gradient in the intensity of sexual selection cannot be the only underlying process that explains the pattern of increasing dimorphism with increasing body size. Instead, sexual selection may be simply one form of a general class of selection processes in which intensity varies with changes in body size. A goal of future research should be the characterization of these selection processes and identification of ones that give rise to patterns parallel to Rensch's rule. Besides the sterile worker castes of ants, other forms of intrasexual dimorphism occur in a wide variety of insect groups. These groups offer numerous opportunities for exploring evolutionary divergence in body size and assessing the universality of the underlying mechanisms responsible for it.

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## LITERATURE CITED

- Abouheif, E. 1998. Random trees and the comparative method: a cautionary tale. *Evolution* 52: 1197–1204.
- and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* 149: 540–562.
- Blanckenhorn, W. U., A. F. G. Dixon, D. J. Fairbairn, M. W. Foellmer, P. Gibert, K. van der Linde, R. Meier, S. Nylin, S. Pitnick, C. Schoff, M. Signorelli, T. Teder, and C. Wiklund. 2007. Proximate causes of Rensch's rule: does sexual size dimorphism in arthropods result from sex differences in development time? *American Naturalist* 169: 247–257.
- Bolton, B. 1995. *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, MA.
- Carlin, N. F. and A. B. Johnston. 1984. Learned enemy specification in the defense recruitment system of an ant. *Naturwissenschaften* 71: 156–157.
- Creighton, W. S. 1966. The habits of *Pheidole ridicula* Wheeler with remarks on habit patterns in the genus *Pheidole* (Hymenoptera: Formicidae). *Psyche* 73: 1–7.
- Donoghue, M. J. and D. D. Ackerly. 1996. Phylogenetic uncertainties and sensitivity analyses in comparative biology. *Philosophical Transactions of the Royal Society of London, Series B* 351: 1241–1249.
- Emlen, D. J. 2000. Integrating development with evolution: a case study with beetle horns. *Bioscience* 5: 403–418.
- and H. F. Nijhout. 2000. The development and evolution of exaggerated morphologies in insects. *Annual Review of Entomology* 45: 661–708.
- Evans, J. D. and D. W. Wheeler. 2001. Gene expression and the evolution of insect polyphenisms. *BioEssays* 23: 1–7.
- Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28: 659–687.
- and R. F. Preziosi. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, *Aquarius remigis*. *American Naturalist* 144: 101–118.
- Feener, D. H., Jr. 1981. Competition between ant species: outcome controlled by parasitic flies. *Science (Washington, D.C.)* 214: 815–817.
- . 1987. Response of *Pheidole morrisi* to two species of enemy ants, and a general model of defense behavior in *Pheidole* (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society* 60: 569–575.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.
- Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41: 18–32.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London, Series B* 326: 119–157.
- . 1992. The uniqueness of the phylogenetic regression. *Journal of Theoretical Biology* 156: 405–423.
- Harrison, R. G. 1980. Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics* 11: 95–118.
- Harvey, P. H. and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- Hölldobler, B. and E. O. Wilson. 1990. *The ants*. Harvard University Press, Cambridge, MA.
- LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* 20: 97–117.
- Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* 34: 292–307.
- Lovich, J. E. and J. W. Gibbons. 1992. A review of techniques for quantifying sexual dimorphism. *Growth, Development and Aging* 56: 269–281.
- Martins, E. P. 1996. Conducting phylogenetic comparative studies when the phylogeny is not known. *Evolution* 50: 12–22.
- and T. Garland. 1991. Phylogenetic analysis of the correlated evolution of continuous characters: a simulation study. *Evolution* 45: 534–557.
- McArdle, B. H. 1988. The structural relationship: regression in biology. *Canadian Journal of Zoology* 66: 2329–2339.
- Moreau, C. S. 2008. Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution* 48: 224–239.
- Oster, G. F. and E. O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton University Press, Princeton, NJ.
- Pagel, M. D. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* 156: 431–442.
- Paradis, E. 2006. *Analysis of phylogenetics and evolution with R*. Springer, New York, NY.
- Pie, M. R. and J. F. A. Traniello. 2006. Morphological evolution in a hyperdiverse clade: the ant genus *Pheidole*. *Journal of Zoology* 271: 99–109.

- Purvis, A., J. L. Gittleman, and H. K. Luh. 1994. Truth or consequences: effects of phylogenetic accuracy on two comparative methods. *Journal of Theoretical Biology* 167: 293–300.
- Quader, S., K. Isvaran, R. E. Hale, B. G. Miner, and N. E. Seavy. 2004. Nonlinear relationships and phylogenetically independent contrasts. *Journal of Evolutionary Biology* 17: 709–715.
- Rensch, B. 1950. Die Abhängigkeit der relativen sexualdifferenz von der Kopergröße. *Bonner Zoologische Beiträge* 1: 58–69.
- . 1959. *Evolution above the species level*. Columbia University Press, New York, NY.
- Roff, D. A. 1986. The evolution of wing dimorphism in insects. *Evolution* 40: 1009–1021.
- Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50: 1766–1774.
- Sempo, G. and C. Detrain. 2004. Between-species differences of behavioural repertoire of castes in *Pheidole* ant genus: methodological artefact? *Insectes Sociaux* 51: 48–54.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. W. H. Freeman and Company, San Francisco, CA.
- Stern, D. L. and D. J. Emlen. 1999. The developmental basis for allometry in insects. *Development* 126: 1091–1101.
- Stubblefield, J. W. and J. Seger. 1994. Sexual dimorphism in the Hymenoptera. Pp. 71–103 in R. V. Short, and E. Balaban eds. *The differences between the sexes*. Cambridge University Press, Cambridge, UK.
- Thornhill, R. and J. Alcock. 1983. *The evolution of insect mating systems*. Harvard University Press, Cambridge, MA.
- Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81: 259–291.
- Webb, T. J. and R. P. Freckleton. 2007. Only half right: species with female-biased sexual size dimorphism consistently break Rensch's rule. *PLoS ONE* 2: e897.
- Wheeler, D. E. 1991. The developmental basis of worker caste polymorphism in ants. *American Naturalist* 138: 1218–1238.
- Wilson, E. O. 1971. *The insect societies*. The Belknap Press of Harvard University Press, Cambridge, MA.
- . 1976a. Behavioral discretization and the number of castes in an ant species. *Behavioral Ecology and Sociobiology* 1: 141–154.
- . 1976b. The organization of colony defense in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 1: 63–81.
- . 1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 16: 89–98.
- . 2003. *Pheidole in the New World: a dominant, hyperdiverse ant genus*. Harvard University Press, Cambridge, MA.
- Zeng, Z.-B. 1988. Long-term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* 42: 363–374.

APPENDIX 1. List of *Pheidole* species included in the study. Species with a trimorphic worker caste are indicated in bold type.

<i>absurda</i>	<i>crassicornis</i>	<i>macrops</i>	<i>sciophila</i>
<i>adrianoi</i>	<i>davisi</i>	<i>mamore</i>	<i>scrobifera</i>
<i>allarmata</i>	<i>dentata</i>	<i>megacephala</i>	<i>senex</i>
<i>amazonica</i>	<i>desertorum</i>	<i>metallescens</i>	<i>sensitiva</i>
<i>artemisida</i>	<i>diana</i>	<i>micula</i>	<i>sicaria</i>
<i>astur</i>	<i>diversipilosa</i>	<i>militicida</i>	<i>sitiens</i>
<i>barbata</i>	<i>dossena</i>	<i>minutula</i>	<i>soritis</i>
<i>bicarinata</i>	<i>erratilis</i>	<i>moerens</i>	<i>sospes</i>
<i>biconstricta</i>	<i>fimbriata</i>	<i>morrisi</i>	<i>spadonia</i>
<i>boltoni</i>	<i>fiorii</i>	<i>nitella</i>	<i>striaticeps</i>
<i>boruca</i>	<i>fissiceps</i>	<i>nitidicollis</i>	<i>subarmata</i>
<i>browni</i>	<i>flavens</i>	<i>obscurithorax</i>	<b><i>tepicana</i></b>
<i>californica</i>	<i>floridana</i>	<b><i>obtusospinosa</i></b>	<i>titanis</i>
<i>caltrop</i>	<i>furtiva</i>	<i>pacifica</i>	<i>tristicula</i>
<i>carrolli</i>	<i>gilvescens</i>	<i>pelor</i>	<i>truncula</i>
<i>casta</i>	<i>granulata</i>	<i>perpilosa</i>	<i>tucsonica</i>
<i>cavigenis</i>	<i>harlequina</i>	<i>pilifera</i>	<i>tysoni</i>
<i>cephalica</i>	<i>hoplitica</i>	<b><i>polymorpha</i></b>	<i>umphreyi</i>
<i>cerebrosior</i>	<i>hyatti</i>	<i>portalensis</i>	<i>vallicola</i>
<i>ceres</i>	<i>indagatrix</i>	<i>prostrata</i>	<i>vinelandica</i>
<i>clementensis</i>	<i>indistincta</i>	<i>psammophila</i>	<i>violacea</i>
<i>clydei</i>	<i>innupta</i>	<b><i>rhea</i></b>	<i>vistana</i>
<i>cocciphaga</i>	<i>jelskii</i>	<i>rhinoceros</i>	<i>xerophila</i>
<i>cockerelli</i>	<i>juniperae</i>	<i>rufescens</i>	<i>yaqui</i>
<i>coloradensis</i>	<i>laselva</i>	<i>rugulosa</i>	
<i>constipata</i>	<i>laticornis</i>	<i>sagittaria</i>	
<i>cramptoni</i>	<i>littoralis</i>	<i>sciara</i>	